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Phylogenetic Systematics of Slit-Faced Bats (Chiroptera, Nycteridae), Based on Hyoid and Other Morphology

THOMAS A. GRIFFITHS[1]

ABSTRACT

The hyoid musculature and hyoid apparatus of bats of the family Nycteridae are described and compared with the hyoid morphology of other bat families described elsewhere. Four hyoid and four nonhyoid apomorphic character states are described within the family. All nycterids share the apomorphic hollowing of the rostrum into a basin, covered by a dermal vertical slit ornamented with the distinctive nycterid "noseleaf." All nycterids also possess a distinctive T-shaped terminal caudal vertebra. All nycterids except *N. arge* share a reduced ceratohyoid insertion and a reduced hyoglossus origin. All nycterids except *N. tragata* and *N. arge* share an epihyal that is reduced in length, a smaller lower second premolar, and a loss of the posterior tragus constriction. A cladistic analysis of the data suggests that the African hispida, macrotis, and thebaica groups form a clade. The Asian bats of the javanica group are a sister group to the hispida-macrotis-thebaica clade. Bats of the African arge group are the most basal lineage within the Nycteridae. This analysis supports separating the more primitive nycterids into an arge group and a javanica group rather than combining them in a single group.

INTRODUCTION

Nycterid bats constitute a small family of insectivorous and carnivorous paleotropical bats. Only one genus, *Nycteris,* is recognized in the family, which contains 12 extant species (Koopman, 1993). The distribution of nycterid species is similar to that of some other Old World bat families in that it is disjunct. Ten nycterid species are found in

[1] Research Associate, Department of Mammalogy, American Museum of Natural History; Professor of Biology, Illinois Wesleyan University, Bloomington, IL 61702-2900 (please send requests for reprints to Illinois Wesleyan address).

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Africa (excepting Saharan Africa but including Madagascar and the adjacent westernmost edge of the Arabian peninsula). Two species are known from the Far East, with combined ranges extending from southern Burma south along the Malay Peninsula through Sumatra, Borneo, Java, and to adjacent smaller islands. Nycterid bats apparently are not well represented in the fossil record, other than from Recent strata of Africa and the Malay region.

Andersen (1912), who used the generic name *Petalia* for the species referred to *Nycteris* today, did an early revision of the Nycteridae. Based on tooth morphology and on the shape of the tragus, Andersen recognized four groups within the family that he termed the javanica group, the hispida group, the aethiopica group (later renamed the macrotis group), and the thebaica group (table 1). Within his javanica group, Andersen included the Indo-Malayan species *Petalia javanica* and *P. tragata* with the African species *P. arge, P. nana,* and *P. major.* Aellen (1959) followed Andersen (1912) in most regards, but on the basis of its unusual upper incisor morphology, he separated the Southeast Asian species *Nycteris javanica* from the remainder of Andersen's javanica group. Aellen recognized five groups within the family Nycteridae (table 1): a javanica group containing only *N. javanica*; an arge group containing the African *N. arge, N. nana, N. major,* the newly described *N. intermedia,* and the Southeast Asian *N. tragata*; and the other groups as originally composed by Andersen (hispida, macrotis, and thebaica). Rosevear (1965) refrained from commenting on the taxonomic relationships of the two East Asian species, confining his remarks to western African *Nycteris.* He recognized four African groups in the family containing the following species: 1) an arge group (*arge, nana, major*); 2) a hispida group (*hispida, grandis*); 3) an aethiopica group (*aethiopica, macrotis, parisii*); and 4) a thebaica group (*thebaica, gambiensis*). Hayman and Hill (1971) followed Aellen's arrangement of groups without further comment. Koopman (1975) observed that the upper incisor morphology of *Nycteris javanica* was not that different from the incisor morphology of Aellen's arge group. Koopman followed Andersen (1912) in reuniting the Asian *javanica* with the African *arge, nana,* and *major* and the Asian *tragata* as a javanica group (table 1). He recognized the other three groups as originally proposed by Andersen, excepting of course that acquisition of additional specimens of a number of species had resulted in a revision of species by himself and others (see table 1). Among other changes, *N. aethiopica* had been recognized by Koopman as being conspecific with *N. macrotis.* This necessitated changing the name of the aethiopica group to the macrotis group (Koopman, 1975). Van Cakenberghe and de Vree (1985, 1993) provided the most recent opinion on the groups within the Nycteridae. Based on a sophisticated multivariate analysis of 20 skull and skeletal measurements, Van Cakenberghe and de Vree recognized five groups within the Nycteridae (table 1). The East Asian species *Nycteris javanica* and *N. tragata* were considered a separate group. An African arge group containing four species was recognized, as was an African macrotis group containing *N. macrotis* and *N. woodi.* The African hispida and thebaica groups were not specifically discussed.

It thus appears that there are either four or five clearly defined groups in the family Nycteridae; if there are five, four are from Africa and one from Southeast Asia. The African arge species and the Southeast Asian javanica species have often been associated with one another (Andersen, 1912; Koopman, 1975), but is this association indicative of a close phylogenetic relationship? Or is it possible these two groups share only primitive (= plesiomorphous) traits and thus would not group together in a cladistic study? Members of the arge and javanica groups have often been characterized as "primitive forest types" (Kingdon, 1974; Koopman, 1975), whereas other groups are considered to have become progressively freer of the forest environment, culminating in the thebaica group which has become adapted to savanna and semidesert environments (Koopman, 1975). Yet no one has ever investigated the relationship between the various *Nycteris* groups to see if this characterization is borne out by a cladistic analysis of morphological (or other) data.

The purpose of this study is to describe the

TABLE 1

Groupings of Species Within the Genus *Nycteris* (*Petalia* of Andersen) by Various Authorities

Column 5 is this study.

Andersen (1912)	Aellen (1959)	Koopman (1975)	Van Cakenberghe/ de Vree (1985, 1993)	Griffiths[a]
javanica group	javanica group	javanica group	javanica group	javanica group
P. javanica	*N. javanica*	*N. javanica*	*N. javanica*	*N. javanica*
P. tragata	arge group	*N. tragata*	*N. tragata*	*N. tragata*
P. arge	*N. tragata*	*N. arge* (incl. *intermedia*)	arge group	arge group
P. nana	*N. arge*	*N. nana*	*N. arge*	*N. arge*
P. major	*N. nana*	*N. major*	*N. nana*	*N. nana*
hispida group	*N. major*	hispida group	*N. major*	*N. major*
P. hispida	*N. intermedia*	*N. hispida* (incl. *aurita*)	*N. intermedia*	*N. intermedia*
P. aurita	hispida group	*N. grandis*	hispida group	hispida group
P. grandis	*N. hispida*	macrotis group	not discussed	*N. hispida*
aethiopica group	*N. aurita*	*N. macrotis* (incl. *aethiopica*)	macrotis group	*N. grandis*
P. aethiopica	*N. grandis*	*N. parisii*	*N. macrotis* (incl. *aethiopica* and *madagascariensis*)	macrotis group
P. macrotis	aethiopica group	*N. woodi*	*N. woodi* (incl. *parisii*)	*N. macrotis*
thebaica group	*N. aethiopica*	thebaica group	thebaica group	*N. woodi*
P. thebaica	*N. macrotis*	*N. thebaica* (incl. *revoili, capensis, damarensis,* and *gambiensis*)	not discussed	thebaica group
P. revoili	thebaica group	*N. vinsoni*[b]		*N. thebaica*
P. capensis	*N. thebaica*	*N. madagascariensis*		*N. gambiensis*
P. damarensis	*N. revoili*			
P. gambiensis	*N. capensis*			
	N. damarensis			
	N. gambiensis			

[a] Groups I would recognize on the basis of this study. Composition of each group follows Koopman (1993) as to which species are valid.

[b] Koopman (1992) subsequently reexamined the type specimen of *Nycteris vinsoni,* reconstituting the shriveled, fire-damaged tragus in the process by adding 70% ethanol. He discovered that the tragus was in fact semilunate rather than pyriform, and he transferred *vinsoni* from the thebaica group to the macrotis group, regarding it as a subspecies of *macrotis.*

hyoid morphology of representative specimens of all available species of nycterid bats (at least one species from each of the nycterid groups). Hyoid data are combined with other morphological data, compared with outgroup data, and are analyzed using cladistic methodology to produce the first phylogeny ever generated for the family Nycteridae. Ultimately, these data will be used to generate a phylogeny for all six families within Koopman's Yinochiroptera (Rhinopomatidae, Emballonuridae, Craseonycteridae, Rhinolophidae, Megadermatidae, and Nycteridae; Koopman, 1984), but that objective must wait until Griffiths and associates complete their dissections of rhinolophid and craseonycterid bats. This paper is the fourth in a series (Griffiths et al., 1991; Griffiths and Smith, 1991; Griffiths et al., 1992; this paper) of which the ultimate aim is to describe the hyoid morphology of representatives of virtually all microchiropteran genera and produce a phylogeny for the entire suborder Microchiroptera.

Materials and Methods

Fluid-preserved museum specimens of the following species were dissected under a binocular dissecting microscope and drawings were made in pencil of all dissections. From the initial drawings, selected drawings were inked for inclusion in this work. All specimens dissected are from the collections of the American Museum of Natural History (AMNH) in New York. Family Nycteridae: *Nycteris arge*: AMNH 49386, 49387, 233876, 233877; *N. gambiensis*: AMNH 237417, 237418 (skull removed, but hyoid region intact); *N. grandis*: AMNH 265825 (skull removed, but hyoid region intact); *N. hispida*: AMNH 150183, 150184, 233878, 233879; *N. intermedia*: AMNH 265707 (skull removed, very little useful information left in hyoid region); *N. macrotis*: AMNH 89449, 89451, 49399, 187288 (formerly *aethiopicus*); *N. thebaica*: AMNH 245150, 245154, 245209, 245210; and *N. tragata*: AMNH 216803, 236195, 247250, 247251. Outgroup comparisons were made with genera of other bat families belonging to Koopman's (1984) Infraorder Yinochiroptera (Rhinopomatidae, Emballonuridae, Craseonycteridae, Rhinolophidae, and Megadermatidae) and other bats as necessary, whose hyoid morphology is described in Sprague (1943), Griffiths (1978a, 1978b, 1982, 1983), Griffiths et al. (1991, 1992), and Griffiths and Smith (1991).

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RESULTS

In each of the following anatomical descriptions, the generalized morphology found in the majority of nycterid species is described first, followed by the nycterid species that are exceptions to the generalized morphology (if any). Finally, the hyoid morphology of other families of yinochiropteran bats that have been dissected is described under Outgroups. In this paper, the term "known bats" refers to chiropteran outgroup species that have been dissected, not to all known bat species.

Hyoid Apparatus (figs. 2, 4, 6)

The hyoid elements of all *Nycteris* specimens examined are similar except for some variation in the size of the elements in the anterior cornu. The basihyal consists of a transverse bar, slightly thicker at its midline than at either tip, with a small entoglossal process projecting posteriorly or dorsally from the midline (the basihyal is a moveable element, so the direction of projection varies

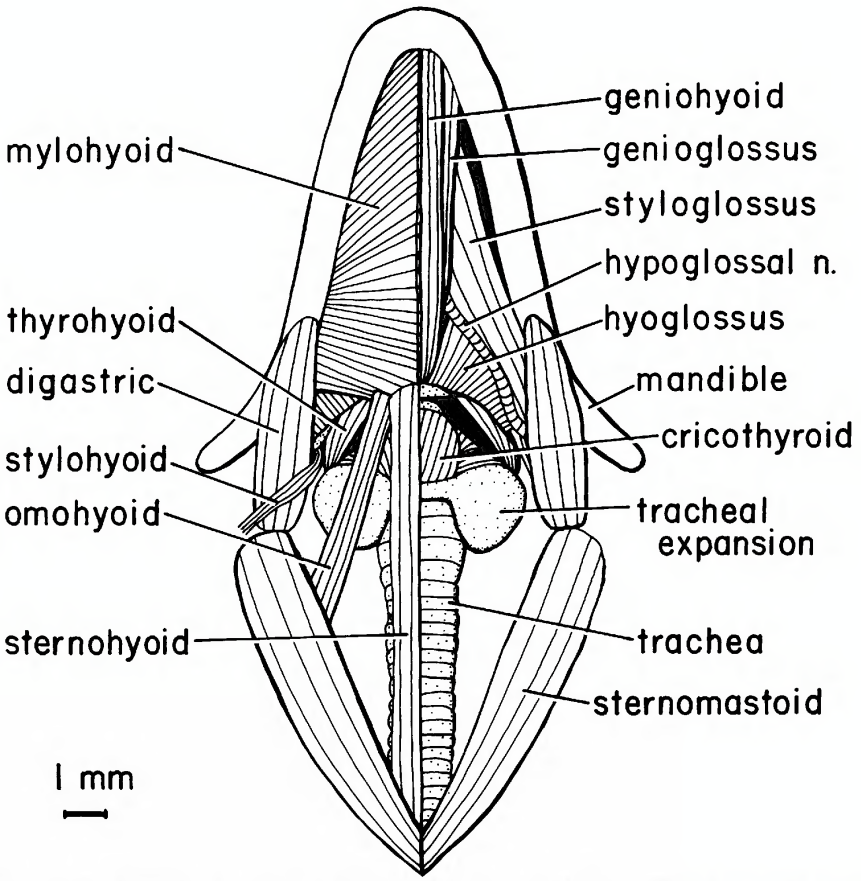

Fig. 1. Ventral view of the superficial hyoid region of *Nycteris arge*. The mylohyoid, stylohyoid, and sternohyoid muscles are removed to show deeper structures on the right side (the bat's left side).

from specimen to specimen, depending on the relative degree of contraction of different hyoid muscles at the time the specimen was prepared). The thyrohyal is fused to the lateral tip of the basihyal on each side; it consists of a long, thin, slightly curved cartilage bar which is otherwise undifferentiated. On the anterior cornu, the ceratohyal and epihyal are straight elements with slightly swollen tips. In *N. arge* and *N. tragata,* the ceratohyal and epihyal elements are approximately the same length. In *N. macrotis, N. hispida, N. grandis, N. gambiensis,* and *N. thebaica,* the epihyal is substantially shorter than the ceratohyal element. The stylohyal in all *Nycteris* examined is a long, thin, sharply curved element with no evidence of an expanded distal foot.

OUTGROUPS: In all other yinochiropteran bats, either the ceratohyal is shorter than the epihyal (in some cases much shorter), or the two elements are approximately the same length (Griffiths and Smith, 1991; Griffiths et al., 1991; 1992).

BRANCHIOMERIC MUSCULATURE

MYLOHYOID GROUP

Muscles of this group are innervated by the mylohyoid nerve, a branch of N. mandibularis, which in turn is a branch of N. trigeminus (V).

M. mylohyoideus
Figures 1, 3, 5

ORIGIN: From the medial surface of the entire length of the body of the mandible.

INSERTION: Into its antimere along the

ventral midline; posteriormost fibers pass deep to the insertion of the omohyoid to insert on the lateral surface of the basihyal.

EXCEPTIONS: The muscle is the same in all nycterids.

OUTGROUPS: In emballonurids (except for *Rhynchonycteris* and *Diclidurus*) and rhinopomatids, the insertion of the mylohyoid is on the ventral midline raphe and the basihyal, and it extends out onto the thyrohyal (Griffiths and Smith, 1991; Griffiths et al., 1991). In the known rhinolophids and all megadermatids, the insertion is on the ventral midline and the lateral basihyal, but not onto the thyrohyals (Griffiths and Smith, 1991; Griffiths et al., 1992).

COMMENTS: This is a solid, substantial and robust muscle that extends for the entire length of the intermandibular space, from the mandibular symphysis to the basihyal. There are no breaks or apoeneuroses in the muscle. No part of the mylohyoid inserts on the thyrohyal elements, except that in one specimen of *Nycteris thebaica* a very few posterior fibers appeared to attach to the medialmost part of the thyrohyal.

M. mylohyoideus profundus

This muscle is absent in all nycterids dissected.

OUTGROUPS: This muscle is not present in any known yinochiropteran bat. It is present in New World phyllostomids (Griffiths, 1982).

M. mandibulo-hyoideus

This muscle is absent in all nycterids dissected.

OUTGROUPS: Sprague (1943), Griffiths and Smith (1991), and Griffiths et al. (1992) report that a mandibulo-hyoideus is present only in three families of bats: megadermatids, rhinopomatids, and rhinolophids. Griffiths and Smith (1991) found that the mandibulohyoid of rhinopomatids is very different from that of rhinolophids and megadermatids in that it possesses a peculiar tendinous connection to the dorsal side of the digastric raphe (Griffiths and Smith, 1991: figs. 1 and 2).

HYOID CONSTRICTOR GROUP

Muscles of this group are innervated by branches of N. facialis (VII).

M. stylohyoideus
Figures 1–6

ORIGIN: By tendon from the posteromedial surface of the lateral tip of the stylohyal element.

INSERTION: Onto the lateral tip of the thyrohyal.

EXCEPTIONS: The muscle is the same in all nycterids.

OUTGROUPS: This muscle is present in most emballonurids and all rhinopomatids, and has the same origin and insertion as described above, with the following exceptions. It is completely absent in *Taphozous* and *Saccolaimus*, and the insertion has shifted to the basihyal in *Peropteryx* and *Peronymus* (Griffiths and Smith, 1991). It is completely absent in the known rhinolophids (including hipposiderines, Griffiths and Smith, 1991), and in most phyllostomids (see Griffiths, 1982). Sprague (1943) reported that this muscle is absent in megadermatids. Griffiths et al. (1992) found it is present (though reduced in size) in the Megadermatidae; its insertion is indirectly onto the basihyal via connective tissue in the basihyal region.

M. jugulohyoideus
Figures 2, 4, 6

ORIGIN: From the paroccipital region of the skull, just posterior (caudal) to the auditory bulla.

INSERTION: Onto the lateral tip of the stylohyal element.

EXCEPTIONS: The muscle is the same in all nycterids. It is a poorly developed muscle in all specimens dissected.

OUTGROUPS: In all other bats, when present, the origin and insertion are the same as in nycterids. It is absent in the more derived genera of emballonurids (Griffiths and Smith, 1991) and in *Cardioderma* (Griffiths et al., 1992).

M. sphincter colli profundus

There is no trace of this muscle, not even fascial tracts, in any nycterid dissected.

OUTGROUPS: This muscle is absent in all emballonurids, rhinopomatids, and all known rhinolophids (rhinolophines and hipposider-

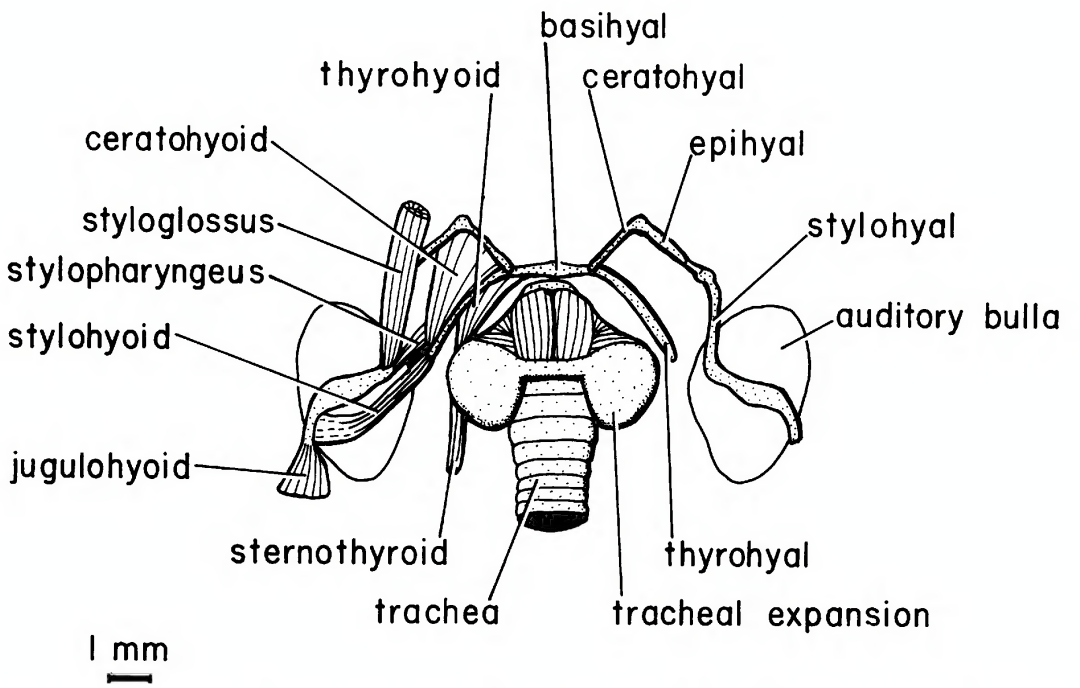

Fig. 2. Ventral view of the deep hyoid region and larynx of *Nycteris arge*. Deeper structures are shown on the right side. The stylohyoid would, in reality, be curving ventrally around the digastricus muscle (removed in this illustration).

ines). It is present as a heavy, robust muscle in megadermatids, with an unusual origin in three of the four genera in the family (Griffiths et al., 1992). In *Megaderma, Cardioderma,* and *Lavia,* the sphincter colli profundus originates posteriorly, from a raphe that bisects the sternohyoid. In *Macroderma,* the sphincter colli originates from the basihyal raphe (as it does in most other bats and most mammals).

M. stylopharyngeus
Figures 2, 4, 6

ORIGIN: From the posteromedial surface of the stylohyal element at about the same point as the styloglossus takes origin (about half way along the length of the stylohyal).

INSERTION: Into the lateral pharyngeal wall, just anterior to the thyropharyngeus.

EXCEPTIONS: The muscle is the same in all nycterids.

OUTGROUPS: The muscle is the same in all known bats (Sprague, 1943; Griffiths, 1982; Griffiths and Smith, 1991).

M. ceratohyoideus
Figures 2, 4, 6

ORIGIN: In most *Nycteris* examined, from the entire anterior surface of the thyrohyal element.

INSERTION: Onto the posterior surface of the ceratohyal element alone (not the epihyal) in most *Nycteris* examined.

EXCEPTIONS: In all specimens of *Nycteris arge* examined and in one of the four *N. tragata,* the origin of this muscle was the distal tip of the thyrohyal rather than the entire anterior surface. In all *N. arge,* the insertion was onto the entire ceratohyal and the medial half of the epihyal.

OUTGROUPS: Griffiths (1982), Griffiths and Smith (1991), and Griffiths et al. (1991, 1992) have summarized the known variation in morphology of this muscle in Old and New World families of bats. The muscle is exceedingly variable even within some species (as, for example, in the origin of *N. tragata* above), and it is probably impossible to determine the plesiomorphous state for Chi-

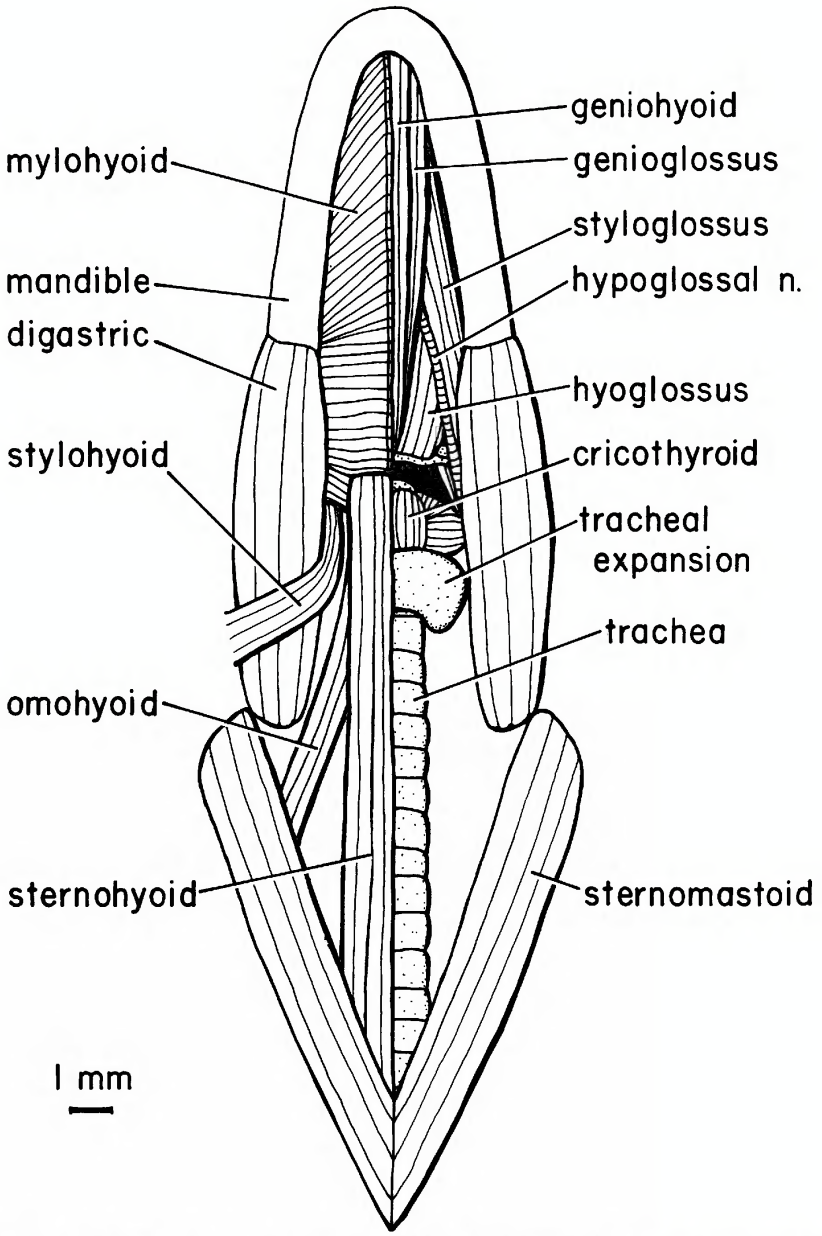

Fig. 3. Ventral view of the superficial hyoid region of *Nycteris tragata.* The mylohyoid, stylohyoid, and sternohyoid muscles are removed to show deeper structures on the right side.

roptera with certainty (see Griffiths and Smith, 1991). Most yinochiropteran bats seem to have an insertion of the ceratohyoid that is onto the entire ceratohyal and part or all of the epihyal. In *Rhinopoma* the insertion is onto the entire posterior surface of both the ceratohyal and epihyal (Griffiths and Smith, 1991). Within the Emballonuridae, in *Taphozous nudiventris,* the insertion is only on the ceratohyal (Griffiths and Smith, 1991), but in *Taphozous melanopogon,* it is on the ceratohyal and medial half of the epihyal (Griffiths et al., 1991). In all New World emballonurid genera, the insertion is on the ceratohyal and the medial half of the epihyal except in *Balantiopteryx,* where it is the cer-

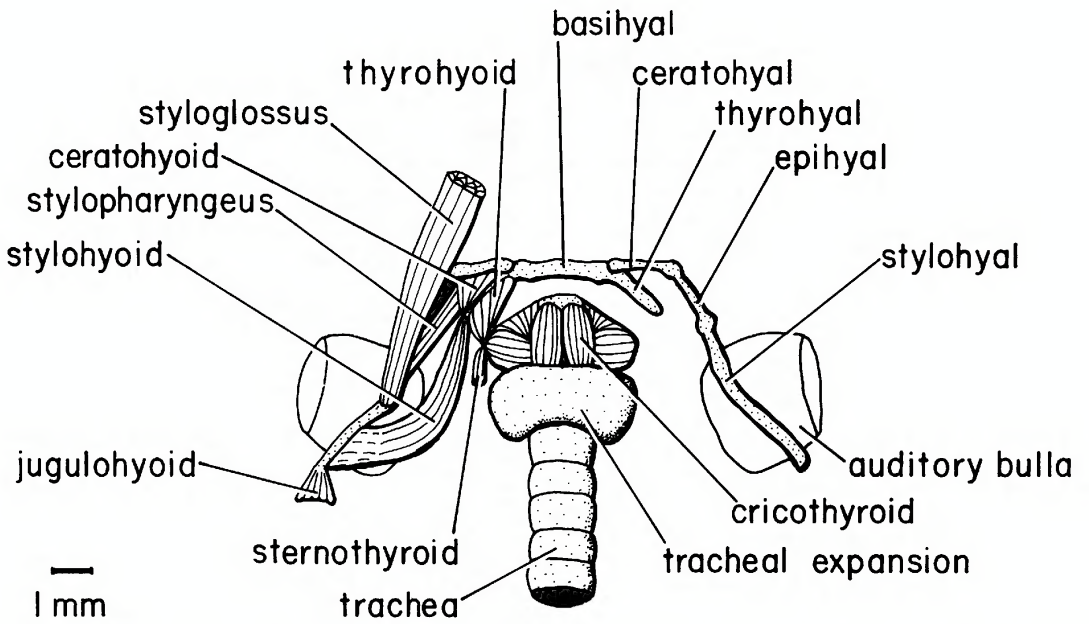

Fig. 4. Ventral view of the deep hyoid region and larynx of *Nycteris tragata*. Deeper structures are shown on the right side. The stylohyoid would, in reality, be curving ventrally around the digastricus muscle (removed in this illustration).

atohyal and medial third of the epihyal (Griffiths and Smith, 1991). In megadermatids this muscle is enormously variable, but in most, the insertion is the ceratohyal and at least some of the epihyal (Griffiths et al., 1992). In rhinolophids that have been examined to date that possess a ceratohyoid muscle, the insertion is onto the lateral half of the epihyal and the medial quarter of the stylohyal (Griffiths and Smith, 1991).

Pharyngeal Constrictor Group

Muscles of this group are innervated by branches of N. vagus (X).

M. hyopharyngeus
Not figured

Origin: From the connective tissue (fascia) in the region of the pterygoid processes.

Insertion: Into the connective tissue of the dorsal pharyngeal midline.

Exceptions: The muscle is the same in all nycterids.

Outgroups: The muscle is the same in all known bats (Griffiths, 1982; Griffiths and Smith, 1991).

M. thyropharyngeus
Not figured

Origin: From the dorsal surface of the thyrohyal element.

Insertion: Into the dorsal pharyngeal midline (the most superficial fibers insert directly into their antimere).

Exceptions: The muscle is the same in all nycterids.

Outgroups: The muscle is the same in all known bats (Griffiths, 1982; Griffiths and Smith, 1991).

M. cricopharyngeus
Not figured

Origin: From the lateral cricoid cartilage and the dorsal surface of the posterior thyroid cartilage process.

Insertion: Into the dorsal pharyngeal midline (the most superficial fibers insert directly into their antimere). The anteriormost fibers run deep to the thyropharyngeus.

Exceptions: The muscle is the same in all nycterids.

Outgroups: The muscle is essentially the

same in all known bats (Griffiths, 1982; Griffiths and Smith, 1991).

Myotomic Musculature

Lingual Group

Muscles of this group are innervated by branches of N. hypoglossus (XII).

M. genioglossus
Figures 1, 3, 5

Origin: From the posterior surface of the mandible just lateral to the mandibular symphysis, deep to the origin of the geniohyoid.

Insertion: Into the ventral midline of the tongue for much of the length of the tongue; the most posterior fibers of the genioglossus turn and pass laterally under the mid hyoglossus.

Exceptions: The muscle is the same in all nycterids.

Outgroups: With minor variations in size and shape, this muscle is the same in all known bats (Griffiths, 1982; Griffiths and Smith, 1991).

M. hyoglossus
Figures 1, 3, 5

Origin: In most *Nycteris,* from the lateral surface of the basihyal.

Insertion: Into the posterolateral tongue, deep to the hypoglossal nerve and the styloglossus muscle.

Exceptions: In *Nycteris arge,* the bulk of the muscle originates from the basihyal, but a significant proportion of the more lateral fibers originate from the anteroventral thyrohyal. In one specimen of *Nycteris tragata,* a few fibers of the hyoglossus took origin from the medialmost thyrohyal.

Outgroups: It seems fairly certain that the plesiomorphous character state for the origin of this muscle is as a broad sheet originating from the lateral basihyal and the anterior thyrohyal. This is the condition found in rhinopomatids and in Old World emballonurids (Griffiths and Smith, 1991). The known rhinolophids have an origin that is exclusively from the basihyal, while most megadermatids have a muscle with a basihyal origin, but with at least a few fibers originating from the anterior thyrohyals. It would appear that independently in all three rhinolophoid families (Rhinolophidae, Megadermatidae, and Nycteridae), there is a trend toward reduction of the origin to the basihyal alone.

M. styloglossus
Figures 1–6

Origin: From the ventral surface of the midpoint of the stylohyal element at the point where it bends sharply (opposite where the stylopharyngeus originates).

Insertion: Into the lateral tongue surface for much of its length.

Exceptions: The muscle is the same in all nycterids.

Outgroups: Most Yinochiroptera have a similar styloglossus. In *Triaenops* and *Rhinonycteris* (Rhinolophidae: Hipposiderinae) the origin is from the distal "foot" of the stylohyal (Griffiths and Smith, 1991). In all megadermatid genera, the insertion is into the posterior tongue (Griffiths et al., 1992).

Medial Ventral Cervical Group

The muscles of this group are innervated by a complex of nerves originating in the anterior cervical region, except for the geniohyoid which is innervated by N. hypoglossus (XII).

M. geniohyoideus
Figures 1, 3, 5

Origin: By short tendon from the posterior surface of the mandible just lateral to the mandibular symphysis.

Insertion: Onto the anterior surface of the basihyal.

Exceptions: The muscle is the same in all nycterids.

Outgroups: Except in megadermatids where the muscle's insertion has "lifted off" the basihyal (see Griffiths et al., 1992), the muscle is the same in all families of yinochiropteran bats.

Comments: The two antimeres of the muscle in nycterids are closely associated, but not fused.

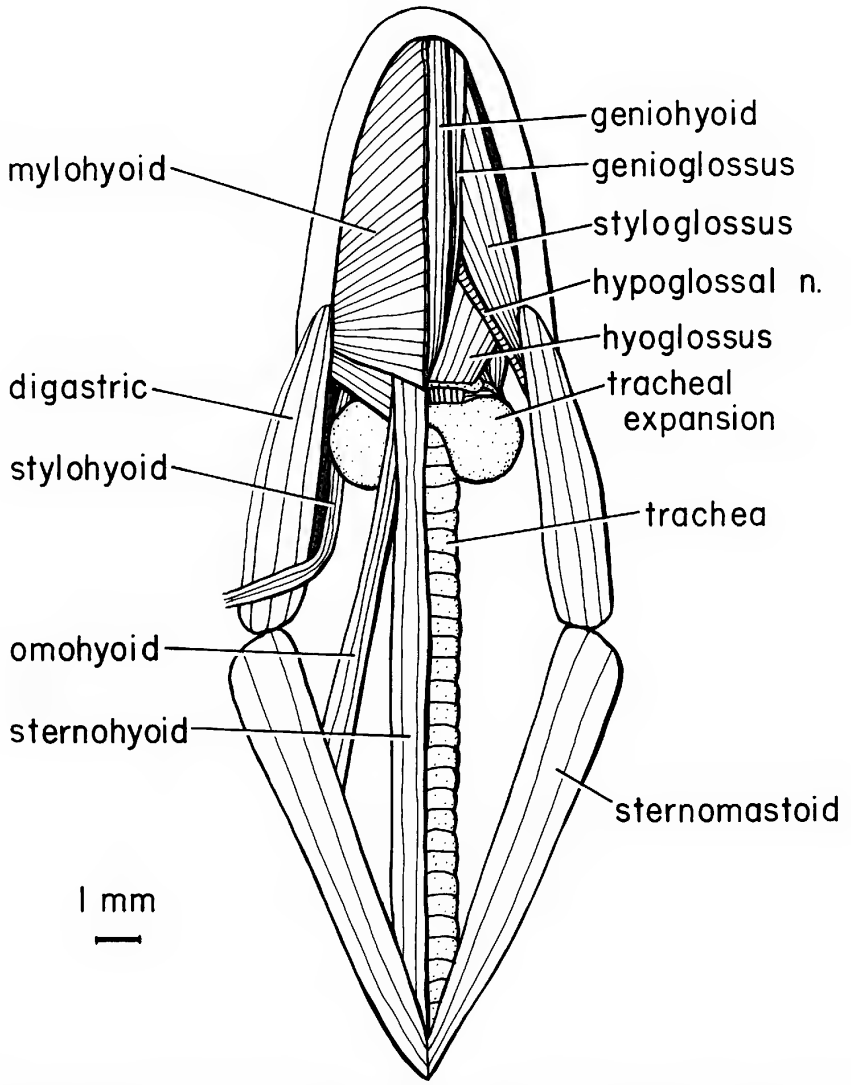

Fig. 5. Ventral view of the superficial hyoid region of *Nycteris macrotis*. The mylohyoid, stylohyoid, and sternohyoid muscles are removed to show deeper structures on the right side.

M. sternohyoideus
Figures 1, 3, 5

ORIGIN: From the lateralmost portion of the anterior surface of the manubrium of the sternum (not from the clavicle or the sternoclavicular joint).

INSERTION: Onto the posterior surface of the basihyal.

EXCEPTIONS: The muscle is the same in all nycterids.

OUTGROUPS: In emballonurids, the origin of this muscle is by two slips, one from the anterior surface of the manubrium and the other from the proximal head of the clavicle. All rhinopomatids, megadermatids, and the known rhinolophids have a sternohyoid that takes origin exclusively from the manubrium of the sternum.

M. sternothyroideus
Figures 2, 4, 6

ORIGIN: Except as noted below, from the lateral manubrium of the sternum, lateral and slightly dorsal to the origin of the sternohyoid.

INSERTION: The muscle passes dorsal to

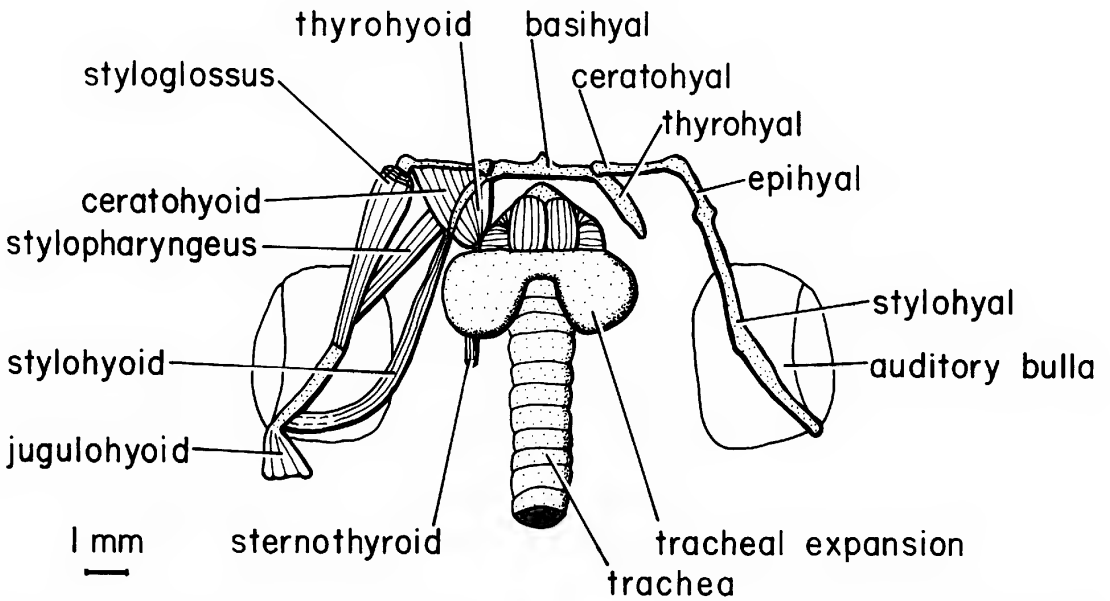

Fig. 6. Ventral view of the deep hyoid region and larynx of *Nycteris macrotis*. Deeper structures are shown on the right side. The stylohyoid would, in reality, be curving ventrally around the digastricus muscle (removed in this illustration).

the tracheal expansion to insert onto the lateral surface of the thyroid cartilage, immediately posterior to the origin of the thyrohyoid.

EXCEPTIONS: In all four *N. thebaica*, in one of the two *N. gambiensis*, in the one specimen of *N. grandis*, and in all four of the *N. tragata* examined, the origin is from the medial head of the clavicle rather than the manubrium.

OUTGROUPS: In rhinopomatids, the origin is from both the manubrium of the sternum and the proximal head of the clavicle. In all emballonurids, the origin is from the medial clavicular head only. In all megadermatids and all rhinolophids examined to date, the origin is from the manubrium of the sternum only. In virtually all mammals, the origin of this muscle is from the manubrium of the sternum (thus the name "sterno"-thyroid).

COMMENTS: The muscle is very reduced in all nycterid specimens examined.

M. omohyoideus

Figures 1, 3, 5

ORIGIN: From the anterior surface of the midpoint of the clavicle.

INSERTION: Onto the posterior surface of the basihyal element, just lateral to the insertion of the sternohyoid.

EXCEPTIONS: The muscle is the same in all nycterids.

OUTGROUPS: The origin of the muscle from the midpoint of the clavicle (and not the scapula as in most mammals) is shared with emballonurids, rhinopomatids, and megadermatids.

M. thyrohyoideus

Figures 1–6

ORIGIN: From the lateral surface of the thyroid cartilage.

INSERTION: Onto the posterior surface of the thyrohyal element.

EXCEPTIONS: The muscle is the same in all nycterids.

OUTGROUPS: The muscle is the same in all known bats (Sprague, 1943; Griffiths, 1982; Griffiths and Smith, 1991).

DISCUSSION

Nycterid bats are enigmatic in several ways. Though there is some evidence from analysis of molecular data that nycterids are a very

old evolutionary line (Pierson, 1986), there is a surprising lack of fossil evidence for the family Nycteridae (Hill and Smith, 1984). On the contrary, the families Megadermatidae, Rhinolophidae, and Emballonuridae, with similar geographical ranges, have relatively rich fossil records that extend well back into the Tertiary (Sigé, 1968, 1976, 1978, 1988; Hand, 1985; Legendre, 1982; Sigé et al., 1982). Furthermore, for a family that appears to be very old, there seems to be remarkably little morphological differentiation within the Nycteridae. Nycterid species are quite similar to one another except for differences in size, shape of the tragus and noseleaf, and upper incisor and lower premolar morphology. Overall similarity of nycterid species is reflected in the fact that all 12 species in the family are placed in a single genus, whereas within the Megadermatidae there are at least four genera (or perhaps five, see Hand, 1985) containing the five extant species.

Although it would be gratifying to report otherwise, the hyoid morphology data also show remarkably little variation within the family Nycteridae. This is in marked contrast to other bat families examined in the past that have shown rich variation in hyoid morphology among genera and species, enabling my associates and I to construct robust cladograms, strongly buttressed with substantial supporting hyoid and other evidence (Griffiths, 1982, Griffiths and Smith 1991; Griffiths et al., 1991; 1992). Nevertheless, there are three hyoid muscles and one hyoid cartilage element that show variation among nycterid species. Interestingly, analysis of both hyoid and nonhyoid morphological data produces a cladogram that requires no postulated reversals and little homoplasy. In other words, the cladogram is quite robust, and it agrees fairly well with what has been suggested in the past about the evolution of the Nycteridae (Kingdon, 1974; Koopman, 1975).

Table 2 summarizes the observed variation in nycterid hyoid morphology. Three myological characters and one osteological character are shown. Character polarity is reasonably easy to determine for characters 1, 2, and 3. Character 4 is slightly more problematic. In the case of character 1, no other known species of yinochiropteran bat has an epihyal with a length shorter than that of the ceratohyal (Sprague, 1943; Griffiths and Smith, 1991; Griffiths et al., 1991, 1992). The derived condition "epihyal shorter than ceratohyal," found in three of the groups of *Nycteris,* seems clearly to be a synapomorphy. For character 2, the only known yinochiropteran bat that has a ceratohyoid muscle inserting only on the ceratohyal element is *Taphozous nudiventris* (Griffiths and Smith, 1991). In all other yinochiropterans, the insertion is more extensive over the elements of the anterior cornu. The derived condition "ceratohyoid insertion onto ceratohyal element only" is found in four groups of *Nycteris.* The third character, "loss of lateral origin of hyoglossus from thyrohyal" is also found in rhinolophids and some megadermatids, but because nycterids and megadermatids each have some family members that have the plesiomorphous condition, the derived morphology seems to have developed independently in each of the three families. It is therefore considered here a synapomorphy of three species groups of *Nycteris.* For character 4, the character polarity is less certain. For virtually all mammals (including all rhinolophid and megadermatid bats), the origin of the sternothyroid muscle is from the lateral manubrium of the sternum. However, for the more primitive (Old World) emballonurids (see Griffiths and Smith, 1991), the origin is the medial clavicular head, and for rhinopomatids, the sternothyroid takes origin from both the manubrium and the medial clavicular head. Because the most immediate outgroup families would presumably be the rhinolophids and megadermatids, it seems most reasonable to assume that the plesiomorphous condition for nycterids is for the sternothyroid muscle to originate from the medial manubrium. Thus *N. tragata, N. grandis,* some *N. gambiensis,* and all *N. thebaica* would share the derived condition of "shift of sternothyroid origin to medial clavicle head." However, it is possible that the condition found in emballonurids is plesiomorphous for the entire Yinochiroptera (see Griffiths et al., 1992). If so, *N. arge, N. hispida,* and *N. macrotis* would possess the derived character state. I consider the latter alternative much less likely, but mention it as a remote possibility.

TABLE 2

Summary of the Apomorphies Used in Constructing the Cladogram (fig. 7).

(+ = apomorphic character state; − = plesiomorphic character state). Outgroups used are described fully in Griffiths and Smith (1991) and Griffiths et al. (1991; 1992).

Character state	Taxon					
	jav	arg	his	mac	the	OUT
Hyoid characters						
1. epihyal reduced to be shorter than the ceratohyal	−	−	+	+	+	−
2. ceratohyoid insertion onto ceratohyal element only	+	−	+	+	+	−[a]
3. loss of lateral origin of hyoglossus from thyrohyal	+	−	+	+	+	−[b]
4. shift of sternothyroid origin to medial clavicle head	+	−	+/−[c]	−	+	−[d]
Nonhyoid characters						
5. saucer-shaped depression on rostrum with dermal slit and nycterid noseleaf	+	+	+	+	+	−
6. T-shaped terminal caudal vertebrae	+	+	+	+	+	−
7. second lower premolar reduced to much less than half the height of the lower first molar	−	−	+	+	+	−
8. loss of pronounced constriction at middle of outer margin of tragus (going from club- or spoon-shaped to either half-moon or inverted pear shaped)	−	−	+	+	+	−

jav = javanica group (*N. tragata*); arg = arge group (*N. arge*); his = hispida group (*N. hispida, N. grandis*); mac = macrotis group (*N. macrotis*); the = thebaica group (*N. thebaica, N. gambiensis*); OUT = outgroup genera in Rhinopomatidae, Emballonuridae, Rhinolophidae, and Megadermatidae.

[a] Plesiomorphic in all outgroup bats used in this study except *Taphozous nudiventris* (Griffiths and Smith, 1991). See text.

[b] Plesiomorphous in all rhinopomatids and the more primitive emballonurids (Griffiths and Smith, 1991). Apparently the apomorphic character state is derived independently in rhinolophids (Griffiths and Smith, 1991), megadermatids (Griffiths et al., 1992), and nycterids (see argument in text).

[c] Apomorphic in the one specimen of *grandis* examined, but plesiomorphic in all *hispida*.

[d] Apomorphic in emballonurids; plesiomorphous in all other outgroups examined (Griffiths and Smith, 1991). Obviously the derived condition developed independently in the Emballonuridae, in *Nycteris tragata*, and in *N. thebaica*.

There are no shared, derived hyoid characters that are found throughout the family Nycteridae, but two nonhyoid characters are often used to define the entire Nycteridae. They are (character 5) possession of the deep saucer on the rostrum of the skull, covered by the deep dermal slit and the nycterid "noseleaf" in life, and (character 6) the T-shaped (or sometimes Y-shaped) terminal caudal vertebra. Both characters are clearly distinctive, derived, and unique to nycterids. A third nonhyoid character (7) shows variability within the family. The second lower premolar is relatively large in all species of the javanica and arge groups, and much smaller in the hispida, macrotis, and thebaica groups. By comparison with yinochiropteran outgroups (all of which seem to have a well-developed second lower premolar), it seems reasonably certain that the reduced premolar is the derived state of character 7. Finally, the variability of the tragus is a bit more difficult to assess. Rhinolophid bats have no tragus. In megadermatids the tragus is bilobed, with one part short and rounded and the other long and thin, quite different from the tragus of all nycterids. The more basal members of the emballonurid tree (as constructed by Robbins and Sarich, 1988, and Griffiths and Smith, 1991) have a tragus that seems to be not too different from the club- or spoon-shaped tragus of the javanica and arge group species. Lacking a better alternative, I tentatively assume that the spoon-shaped morphology is plesiomorphous for nycterids. Loss of the midpoint constriction results in a broader tragus, either semilunar or pyriform (inverted pear shaped). Which

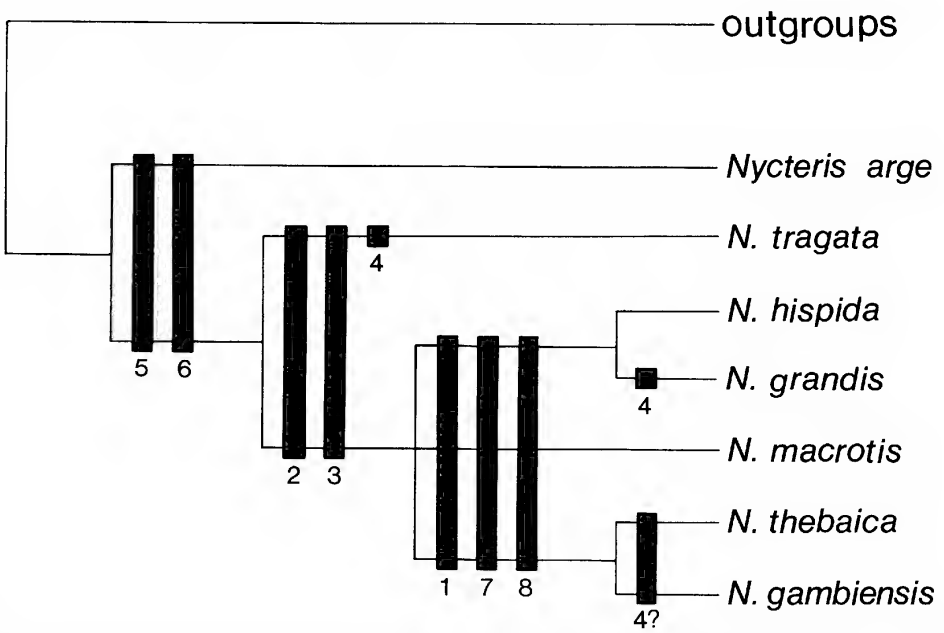

Fig. 7. Cladogram showing phylogenetic relationships among species of nycterid bats. Numbers on bars refer to synapomorphies listed in table 2. There is only one postulated convergent event suggested (character 4) and no reversals are necessary. *Nycteris hispida* and *N. grandis,* and *N. thebaica* and *N. gambiensis* are grouped together on the basis of the derived characters that define their respective species groups (see Koopman, 1975; Van Cakenberghe and de Vree, 1985, 1993).

type of broader tragus gave rise to the other probably cannot be determined.

The cladogram generated from these data is shown in figure 7. No derived hyoid characters support the monophyly of the family, but two nonhyoid characters (facial slit and the terminal caudal vertebra) do so quite well. Interestingly, the East Asian *N. tragata* shares two derived character states with the African hispida, macrotis, and thebaica species. The restricted insertion of the ceratohyoid muscle and the restricted origin of the hyoglossus muscle indicate that *tragata* is more closely related to the three derived African groups than any of these are to the African arge group. The monophyly of a clade containing hispida, macrotis, and thebaica species is supported by the reduction of the length of the epihyal, by the reduction of the second lower premolar, and by the loss of the constriction on the outer margin of the tragus. The most parsimonious treatment of character state 4 (shift of sternothyroid origin to medial clavicle head) is to assume that the derived condition occurred independently in the line leading to *tragata,* in *grandis,* and the line leading to *thebaica* and *gambiensis* (though one *gambiensis* specimen examined shows the plesiomorphous state, so the synapomorphy is shown as 4? on figure 7).

It is interesting to see how well this cladogram for nycterids corresponds with what has been hypothesized about nycterids in the past. The forest-dwelling *Nycteris arge* species line is at the base of the cladogram, suggesting that it is the most primitive of the extant nycterids, just as Kingdon (1974) and Koopman (1975) suggested. The open savanna to semiarid species *Nycteris thebaica* is among the more derived nycterids, in agreement with Koopman's (1975) hypothesis that the thebaica group is the most derived within the nycterid family. Finally, the intermediate position of *N. tragata* on the cladogram might explain the varying treatment that different authors have given to the East Asian species in the past (Table 1). Perhaps Andersen (1912) and Koopman (1975) combined the East Asian species with the arge African species on the basis of primitive characters shared

by the two groups, whereas the analyses by Van Cakenberghe and de Vree (1985, 1993) emphasized the evolution of the javanica group species away from the primitive arge species, prompting them to place *N. javanica* and *N. tragata* in a separate group. The cladistic analysis performed here supports the placement of the African arge species and the East Asian javanica species into different species groups (table 1, column 5).

If the cladogram presented here (fig. 7) is correct, it would appear that the African arge group species represent the most ancient line of nycterids still alive today. Presumably another nycterid line evolved in Africa or the Far East (or perhaps somewhere in between), and spread either eastward to the Far East or westward into Africa (or both). This second line in turn split, leaving bats we know today as the javanica group isolated in the Far East and another line in Africa that became the hispida-macrotis-thebaica clade. Bats of the arge and javanica groups retained much of the primitive morphology of their common ancestors, whereas the hispida-macrotis-thebaica bats evolved new traits of the teeth, noseleaf, tragus, and perhaps other traits of which we are as yet unaware.

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